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RELATIVE ABUNDANCE AND SEASONAL CHANGES IN THE MACROZOOPLANKTON OF THE LOWER SWAN ESTUARY IN SOUTH-WESTERN AUSTRALIA

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ABSTRACT

Macrozooplankton, *i.e.* plankton collected with a 500 μm mesh net (Kennish 1990), was sampled in twelve consecutive months at three sites, located 0.3 (site A), 2.5 (site B) and 7.2 km (site C) from the mouth of the 7.5 km long entrance channel of the Swan Estuary. The macrozooplankton community underwent marked seasonal changes in abundance, with concentrations at particularly sites A and B increasing markedly between November and January, as water temperatures rose towards their annual maxima. Concentrations then fell precipitously at each site in February, before rising sharply again at the two downstream sites (A and B) in April. These trends reflected to a large extent those exhibited by the cladoceran *Penilia avirostris*, which contributed 80.7% to the total number of individuals collected during the study. The other main contributors were *Acartia (Acartiura)* sp. (3.4%), leucosiid (brachyuran) zoea (2.0%), the larvacean *Oikopleura dioica* (1.3%), anomuran crab zoea (1.2%), the penaeid *Lucifer hanseni* (1.1%) and the zoea of the brachyuran *Halicarcinus ovatus* (1.1%). Crustaceans contributed about three quarters of the approximately 100 species collected, with the copepods, most of which were calanoids, contributing 21 of those species. The majority of the species were marine, which accounts for the progressive decline in the concentrations of the macrozooplankton in an upstream direction, with the numbers at sites A, B and C contributing 58.0, 34.0 and 8.0%, respectively, to the total number obtained from all sites.

INTRODUCTION

The composition of the zooplankton, and occasionally also the seasonal changes in that composition, have been studied in some estuaries in eastern Australia (Kott 1955; Bayly 1965; Arnott and Hussainy 1972; Neale and Bayly 1974; Nyan Taw and Ritz 1978; Griffiths 1983). The only comparable investigations that have been carried out on the zooplankton of the estuarine waters of south-western Australia is work on the broad taxonomic groups and main species in the Peel-Harvey Estuary (Lukatelich 1987), and the various studies on the main copepod species in the Swan Estuary (Bhuiyan 1966; Hodgkin and Rippingale 1971; Rippingale and Hodgkin 1974; Rippingale 1987). Moreover, apart from limited data in two reports (Environmental Resources of Australia 1971, 1973), there is no information on the composition and seasonality of zooplankton in the inshore, coastal marine waters of this region.

Information on the composition and seasonality of zooplankton in the estuarine and marine environments in south-western Australia is crucial for constructing detailed food webs for the

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waters in this region. In this context, it is noteworthy that three of the commercially important fish species in south-western Australia, namely the anchovy *Engraulis australis*, the sandy sprat *Hyperlophus vittatus* and the Western Australian pilchard *Sardinops neopilchardus*, are zooplanktivores (Gaughan, unpublished data), and that these species are common in the estuarine as well as marine waters of this region (Loneragan *et al.* 1989; Potter *et al.* 1990).

The zooplankton has been separated into a number of categories, according to the mesh size used for collecting the samples (Kennish 1990). The zooplankton retained by 502 µm mesh are referred to as macrozooplankton. The 500 µm mesh that was used by Gaughan *et al.* (1990) to sample ichthyoplankton at three sites in the lower Swan Estuary over twelve consecutive months, yielded a large bycatch of the invertebrate components of the macrozooplankton. It should be recognized, however, that many individuals of the smaller taxa, such as *Acartia* species and the zoea of various crab species, would have tended to pass through the 500 µm mesh, and thus, in the context of the zooplankton as a whole, they would be under-represented in these samples. At the same time, however, the numbers of such taxa were still sufficiently large to provide data on the way in which their relative abundance varied seasonally and with different regions in the lower estuary.

This paper provides a semi-quantitative checklist of the taxa that were found in the macrozooplankton during twelve consecutive months of sampling in the lower Swan Estuary. It also describes the seasonal trends in abundance exhibited by both the macrozooplankton community and its major taxa, and their relationships to salinity and temperature.

MATERIALS AND METHODS

The lower region of the Swan Estuary comprises a narrow 7.5 km long channel, ranging from 200 to 600 m in width. Samples were collected monthly between May 1986 and April 1987 at sites A, B and C in the lower Swan Estuary, the mid-points of which were located 0.3, 2.5 and 7.2 km from the estuary mouth, respectively, and where the average water depth was 10 m. Full details of the location of these sampling sites and of the sampling regime are given in Gaughan *et al.* (1990).

In brief, sampling, which was carried out in the third quarter of each month, commenced 1-2 hours after sunset and was completed at all three sites within the next 1.5 hours. Samples were collected with a pair of conical nets towed behind a power boat and against the current. Each net was 2 m long and had a mouth diameter of 0.6 m. A stepwise oblique tow (Austin 1976) of 10 minutes duration was made upwards at each site from a depth of 8 m to just below the surface at a speed of *ca* 1 m s^{-1}. The volume of water filtered was measured with a flowmeter fitted in the mouth of one of the nets. The average volume of water sampled by each net was 85 m^3. The nets were washed at the end of each tow, and the samples fixed in 10% formalin and seawater. Surface and bottom salinities and temperatures were recorded at each site at the time of sampling.

Samples were sorted under a dissecting microscope and the taxa identified and counted. Due to the large numbers of organisms usually present, subsampling was carried out employing the method of Wooldridge (1977), whereby the sample was made up to a predetermined volume (500, 750 or 1000 ml) in a large beaker, through which a stream of air was passed to facilitate thorough mixing. A wide-mouthed pipette was used to extract up to five 25 ml subsamples in order to obtain at least 300 individuals of the dominant taxa in the macrozooplankton. The numbers of macrozooplankton taken by each net at each site were standardized by conversion to a concentration, *i.e.* numbers per m^3. The mean of the concentrations for the two nets at each site was then recorded. These concentrations were used to calculate the percentage contributions of the main taxa at each of the three sites to the respective total numbers of those taxa from all three sites and the contribution of all macrozooplankton taxa at each site to the total number of all those taxa.

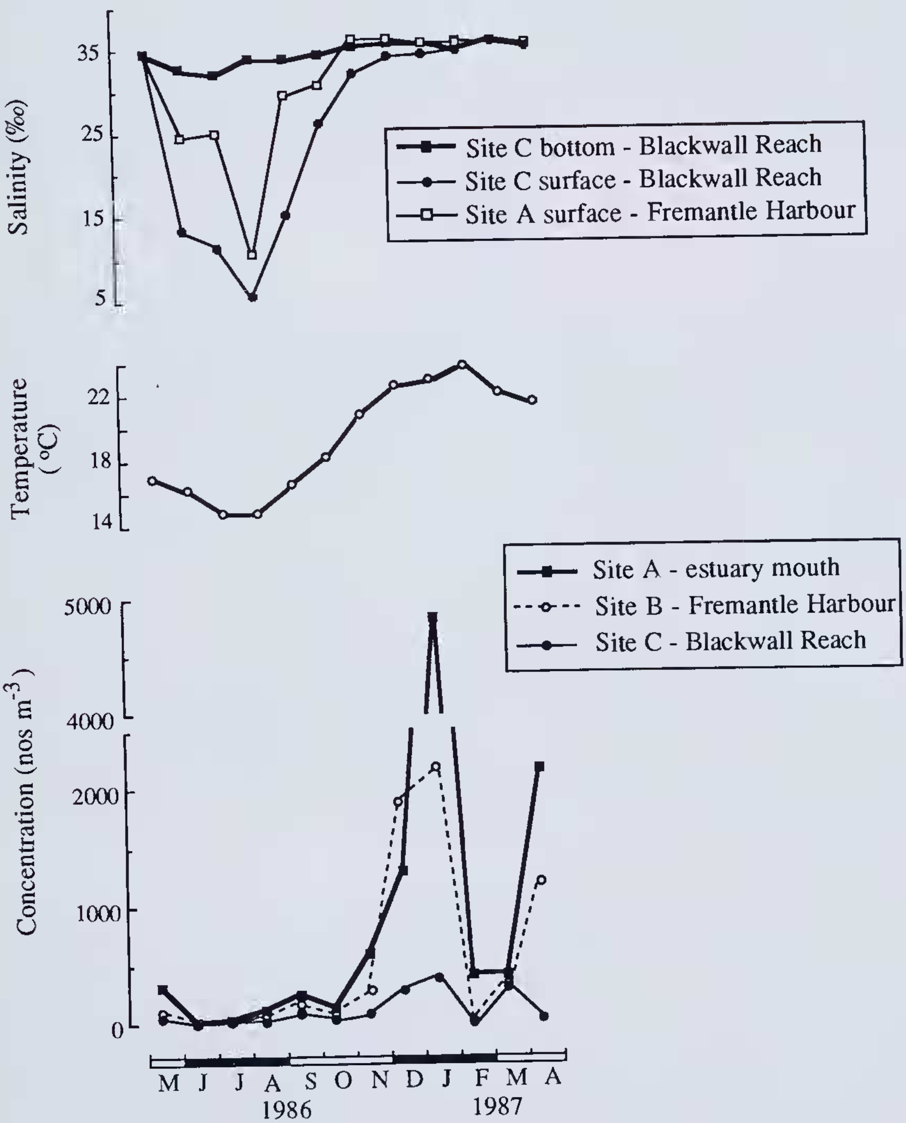

Figure 1 Salinities, water temperatures and concentrations of macrozooplankton in the lower Swan Estuary between May 1986 and April 1987. N.B. Surface salinity at site B was very similar to that at site A, and at both sites A and B the salinity at the bottom was close to 35‰ throughout the year.

RESULTS

Environmental conditions

The trends shown by salinity and water temperatures in the lower Swan Estuary during this study are described in Gaughan *et al.* (1990). In brief, bottom salinities at each of the sites were always greater than 31‰, and were usually of full-strength seawater (35‰) at sites A and B towards the mouth of the estuary (Figure 1). During winter, *i.e.* the wet season, the surface salinity at each site, and particularly at site C, declined markedly. Thus, in August, surface salinity decreased to 10‰ at sites A and B and to as low as 5.4‰ at site C (Figure 1). At each site, the surface salinities increased during spring and by December approached 35‰.

Temperatures at the surface and the bottom of the water column at each of the three sites in any given month never differed by more than 1°C. Mean temperatures in the lower estuary declined from 17.0°C in May 1986 to *ca* 15°C in July and August, before gradually rising to reach a peak of *ca* 24°C in February 1987 (Figure 1).

Macrozooplankton composition

Approximately 100 species were represented in the macrozooplankton of the lower Swan Estuary, of which 17 could be identified to a particular species and a further 19 to genus. The Crustacea contributed the majority (76%) of the macrozooplankton taxa in the lower Swan Estuary. Since the majority of the species could not be identified to species, they were grouped into broader groups, with the result that *ca* 60 "taxa" were enumerated in this study (Table 1).

Several of the taxa that could be identified to species or genus were recorded for the first time in south-western Australia. These included the mysids *Doxomysis* sp. and *Rhopalophthalmus* sp. Furthermore, some taxa, including *Acartia (Acartiura)* sp. and *Haplostylus* spp., were represented by undescribed species or at least by species that were new for Australia (D. McKinnon, T. Wooldridge, pers. comm.).

The most diverse group within the zooplankton in the lower Swan Estuary was the Copepoda, which comprised at least 21 species, the majority of which were holoplanktonic, *i.e.* species which spend their entire life in the plankton, and most of which were calanoids (Table 1). The Cladocera, the other main group of holoplanktonic species, contributed a further five species, of which four were marine and the fifth, a species of *Daphnia*, was derived from freshwater inflow in winter. The zoeal stages of crabs were also well represented in the macrozooplankton, with at least seven species, belonging to the Anomura and the Brachyura, being found.

Relative contributions of the dominant taxa

Seven taxa each contributed at least 1.0% to the total numbers of the macrozooplankton, which was about 1.6 million individuals, and these collectively contributed 90.8% to that total. *Penilia avirostris* was by far the dominant member of the macrozooplankton, contributing 80.7% to the total numbers. The other abundant taxa and their relative contributions to the total were *Acartia (Acartiura) sp.* (3.4%), leucosiid (brachyuran) zoea (2.0%), *Oikopleura dioica* (1.3%), anomuran crab zoea (1.2%), *Lucifer hanseni* (1.1%) and *Halicarcinus ovatus* zoea (1.1%). It should be recognised, however, that *Acartia* (*Acartiura*) sp. and leucosid, anomuran and *H. ovatus* zoea do not reach a large size and would thus not have been sampled efficiently by our 500 μm net. Thus, the above percentage contributions refer to the situation in the macrozooplankton and not to that in the water column.

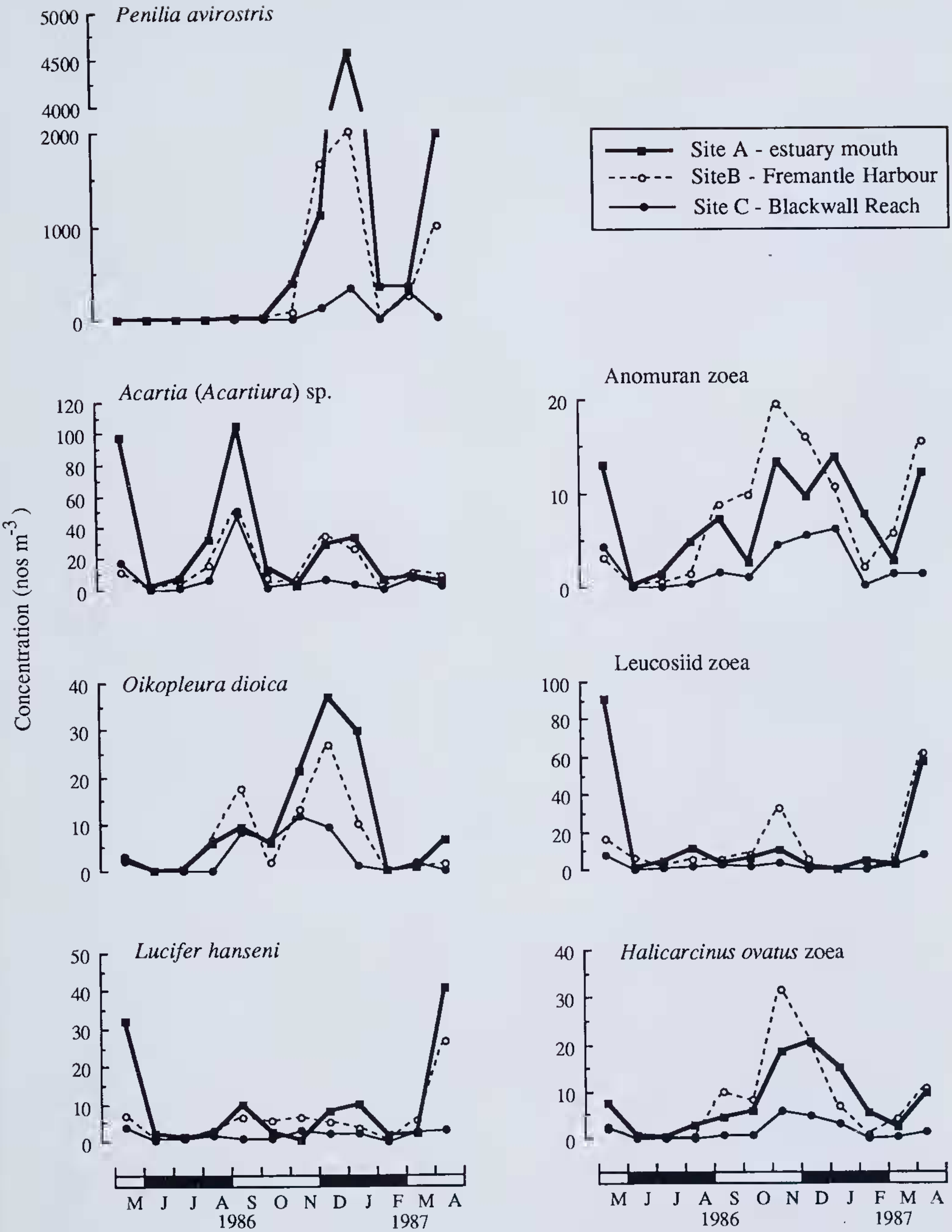

Figure 2 Monthly concentrations of the seven most abundant taxa in the macrozooplankton in the lower Swan Estuary between May 1986 and April 1987.

Table 1 Relative mean monthly concentrations of macrozooplankton in the lower Swan Estuary between May 1986 and April 1987. Concentrations (nos m^{-3}) are given as +, < 1.0; 1, 1 -19; 2, 20-99; 3, 100-999; and 4, > 1 000.

	M	J	J	A	S	O	N	D	J	F	M	A
Platyhelminthes												
Turbellaria	+		+									
Coelenterata												
Hydromedusae	1		+	1	1	+	1	1	1	1	1	1
Cubomedusae											+	
ephyra	+	+	+	+	+	+		+			+	+
Annelida												
Polychaetes												
larvae	2	+	1	1	1	1	1	1	+	1	+	+
adults	+	+	+	+	+	+	+	+		+		
Mollusca												
Gastropoda	1	+	+	1	1	1	+	+	1	1	+	1
Bivalvia		+	+	+		+			+	+	+	+
Chelicerata												
Pycnogonida	+		+	+	+	+	+	+	+	+	+	+
Crustacea												
Branchiopoda												
Cladocera												
Penilia avirostris	1		1	+	2	1	3	4	4	3	3	4
Pseudevadne tergestina	+		+	+	2	2	2	2	2	1	1	1
Evadne nordmanni							+	+				
Podon intermedius	1		1	+	2	1	2	1	1		+	1
Daphnia sp.				+								
Ostracoda	1	+	+	1	1	1	1	1	1	+	+	+
Copepoda												
Calanoida												
Acartia (*Acartiura*) sp.	2	1	1	2	3	1	1	2	2	1	2	1
Acartia sp.	1		+	1	1	1	1	1	+		1	+
Bestiola similis	+						+	1	+	+		1
Centropages australiensis	+		+	+		1	1	2	+	+	1	1
Centropages orsini												
Eucalanus sp.	+		+	+			+					+
Gladioferens imparipes	+	+	+	+	+							
Labidocera cervi	+	+	+	1	+	+	1	1	+	+	+	1
Paracalanus indicus	+	+	+	+	1	+	+		+	+	+	+
Pontellopsis sp.					+	+		+			+	+
Sulcanus conflictus	+	+	1	1				+				
Temora turbinata	1	+	1	2	2	+						
Temora discaudata	+										+	+
Tortanus spp.	1		+	+	+	+	+	+	1	+	+	1
Cyclopoida												
Oithona spp.	1		+	+	1	+	+	1	+		+	+
Corycaeus sp.	+	+	+	+	+	+	+	+	+			1
others			+	+		+	+		+		+	+

Table 1 (cont.)

	M	J	J	A	S	O	N	D	J	F	M	A
Harpacticoida												
Peltidium sp.	+	+	+	+	+	+	+					
others		+			+	+	+	+			+	
Cirrepedia												
nauplii	1		+	1	1	2	2	2	1	+	+	1
Malacostraca												
Leptostraca												
Nebalia sp.	+					+	+	+	+	+		+
Stomatopoda												
Squilla sp. antizoea						+	+	+	+		+	+
Decapoda												
Penaeidea and Caridea												
Sergestidae												
Lucifer hanseni	2	1	1	1	2	1	1	2	2	1	1	2
larvae (mysis stage)	2	1	1	2	2	2	2	3	3	1	2	2
Panulira												
phyllosoma							+	+				
Anomura												
Porcellanid zoea	+		+		+	1	1	1	1	1	1	1
other zoea	2	+	1	1	2	1	2	2	2	1	1	2
megalopae	1	+	+	1	1	+	+	1	1	+	1	1
Brachuyra												
Leucosiid zoea	3	1	1	2	1	1	2	1		1	1	3
Halicarcinus ovatus zoea	1	+	+	1	1	1	2	2	2	1	1	2
Portunus pelagicus zoea					+	+	1	1	2	2	1	+
unidentified zoea				+	1	1	2	2	2	1	1	1
Mysidacea												
Doxomysis sp.	+	+	+	+	+	+	+	+	+	+	+	+
Haplostylus spp.	+	+	+	+	+	+	+	+	+	+	+	+
Rhopalophthalmus sp.	+	+	+	+		+			+	+	1	+
juveniles	+	+	+	+	+	+	+	+	+	+	+	+
Cumacea	+	+	+	1	1	1	1	+	+	+		+
Tanaidacea	+	+	+	+	+	+	+	+	+	+	+	+
Isopoda	+	+	+	+	+	+	+	+	+	+	+	
Amphipoda												
Caprellidae	1	+	+	+	+	+	+	+	+	+	+	1
others	1	1	1	2	1	2	2	1	1	1	1	1
Echinodermata												
Ophiuroidea	+											+
Asteroidea	+											
unidentified larvae	+	+									+	+
Chaetognatha												
Sagitta spp.	1	+	+	+	+	+	1	1	+	+	+	1
Urochordata												
Ascidacea												
larvae	1	+	+	+	+	+						+
Thaliacea										+		+
Larvacea												
Oikopleura dioica	1	+	+	1	2	1	2	2	2	+	1	1

Distribution and seasonality of the macrozooplankton

It was originally intended to use the concentrations of the macrozooplankton community and its main component taxa at sites A, B and C to provide overall mean concentrations for both the community and the most abundant species in the lower Swan Estuary. However, the data in Figures 1 and 2 show that, while the seasonal trends exhibited by the concentrations at each of the three sites were very consistent, the concentrations at each site differed markedly in magnitude in certain months. Since the concentrations at the three sites are considered to reflect the relative abundances of the macrozooplankton in the different regions of the lower estuary, they have been plotted separately.

The concentrations at each site rose from less than *ca* 11 individuals m^{-3} in June 1986 to form a small peak in September and then increased markedly after October to produce a far more prominent peak in December and January. Furthermore, the concentrations of 4,834, 2,116 and 398 individuals m^{-3} recorded in January at sites A, B and C, respectively, represented the maximum annual monthly concentrations at each of those sites (Figure 1). A precipitous decline in the concentration of macrozooplankton occurred at each site in February 1987, with only 420 individuals m^{-3} being recorded at site A and less than 15 individuals m^{-3} at sites B and C. Although the concentrations of macrozooplankton subsequently increased markedly to over 1,000 individuals m^{-3} at sites A and B in April, there was no such increase at site C.

The very high concentrations of macrozooplankton at the three sites in December and January accounts for the fact that the numbers collected in these two months contributed *ca* 60% to the total number of macrozooplankton collected from the lower Swan Estuary during the twelve months of this study. Since the numbers in April contributed a further 19%, 79% of the annual total number of macrozooplankton was recorded in just three months.

Macrozooplankton was most abundant at site A in the estuary mouth in every month except December. Moreover, the concentrations of macrozooplankton were lower at site C at the upstream end of the lower estuary than at sites A or B in every month. The abundance of macrozooplankton thus decreased in an upstream direction, with the differences between the upstream site (C) and the two downstream sites (A and B) being particularly pronounced in December, January and April. The relative contribution by the numbers at sites A, B and C to the total numbers of macrozooplankton were 58, 34 and 8%, respectively (Table 2).

Table 2. The relative proportions of the total macrozooplankton and of each the seven most abundant taxa obtained from each of the three sites in the lower Swan Estuary between May 1986 and April 1987.

Taxa	Percent at site A	Percent at site B	Percent at site C
Penilia avirostris	60.4	34.4	5.2
Acartia (Acartiura) sp.	56.3	27.8	15.9
Oikopleura dioica	49.6	33.5	16.9
Lucifer hanseni	55.2	34.3	10.5
Anomuran zoea	42.4	44.7	12.9
Leucosiid zoea	53.6	38.8	7.6
Halicarcinus ovatus zoea	44.8	45.6	9.6
Total macrozooplankton	58.0	34.0	8.0

Distribution and seasonality of the main taxa

The concentrations of *Penilia avirostris, Acartia (Acartiura)* sp., leucosiid zoea, *Oikopleura dioica* and *Lucifer hanseni* each declined in an upstream direction. Although the concentrations of the zoea of both *Halicarcinus ovatus* and anomurans were also lowest at site C, they did not show any consistent trend to be greater at site A than at site B (Table 2). The total numbers of each of these seven abundant taxa at site A near the estuary mouth each contributed at least 42% of the total numbers of these taxa from all the sites. In contrast, the numbers of none of these seven taxa at site C at the upstream end of the lower estuary contributed more than 17% to the overall numbers of their respective taxa (Table 2).

Penilia avirostris dominated the macrozooplankton of the lower Swan Estuary from November 1986 to April 1987 and was particularly abundant at the two downstream sites, *i.e.* A and B (Figure 2). This point is emphasised by the fact that the maximum monthly concentrations of 4,500 and 2,000 individuals m^{-3} at sites A and B, respectively, which were recorded in January, were far greater than the maximum monthly concentration of 340 individuals m^{-3} at site C.

Acartia (Acartiura) sp. was present at each site in the lower Swan Estuary throughout this study and was usually more abundant towards the estuary mouth (Figure 2). However, the differences between the sites were only pronounced at the times of peak abundance in May and September, at which times this species was the numerically dominant member of the macrozooplankton.

Oikopleura dioica was present throughout the lower estuary in all months except June, and was the most abundant of those species that were not crustaceans. It was particularly abundant between November and January and, in most months, was more abundant at sites A and B than at site C. The highest concentration of *O. dioica* recorded in the lower estuary was 36 individuals m^{-3} at site A in December 1986.

Lucifer hanseni was present at all three sites in the lower Swan Estuary throughout the sampling period and was the most abundant taxon in June 1986. This species peaked in abundance in autumn (May 1986 and April 1987), when concentrations exceeded 30 individuals m^{-3} at the estuary mouth (Figure 2). *Lucifer hanseni* was usually most abundant at the estuary mouth and the maximum concentration at site C never exceeded 3.5 individuals m^{-3}.

Anomuran crab zoea were present at each site in each month of sampling, with the concentrations typically being greatest at sites A and B (Figure 2). These zoea were most abundant from November to January and in May and April. The highest monthly concentration of anomuran zoea in the lower Swan estuary during this study was 20 individuals m^{-3} at site B in November.

Leucosiid zoea were found in the lower Swan Estuary in all months except January 1987 and were usually present at each site (Figure 2). Concentrations of leucosiid zoea peaked in April and May, *i.e.* autumn, at which time concentrations greater than 55 individuals m^{-3} were recorded at either or both of sites A and B. Concentrations of leucosiid zoea were usually least at site C, where the maximum monthly concentration was 8 individuals m^{-3}.

Halicarcinus ovatus zoea were present at each site in the lower estuary in all months except June, when they were found only at site A (Figure 2). They were particularly abundant between November and January and, in most months, were more abundant at sites A and B than at site C. The highest monthly concentration of *H. ovatus* zoea recorded in the lower estuary was 31 individuals m^{-3} at site B in November 1986.

As with the above seven most abundant taxa, many of the other taxa were also present in the lower Swan Estuary for much of the year, although generally only in small concentrations (Table 1). Most of these taxa were more abundant at sites A and B near the estuary mouth than at site C at the upstream end of the lower estuary.

DISCUSSION

Composition

It must be remembered that the quantitative values given in this paper for the concentrations of the different taxa, and thus their contributions to the zooplankton community, have been derived from data collected using a 500 µm mesh. While these concentrations are valid for the macrozooplankton *sensu stricto*, they do not fully reflect the concentrations of the smaller taxa in the zooplankton as a whole. However, it is worth reiterating that the abundant smaller taxa were still well represented and that five of these taxa ranked amongst the seven most abundant taxa caught. Indeed, the composition of the holoplankton in the lower Swan Estuary was similar to that recorded in zooplankton surveys carried out in estuarine and inshore waters elsewhere in Australia, despite the fact that the mesh sizes used in the present and those other studies ranged from 158 to 500 µm (Rochford 1951; Kott 1955; Bayly 1965; Arnott and Hussainy 1972; Neale and Bayly 1974; Griffiths 1983; Kimmerer *et al.* 1985; Kimmerer and McKinnon 1985). Thus, the copepods and cladocerans that were found in the lower Swan Estuary were often represented by either the same species or at least the same genera in eastern Australian estuaries (Bayly 1975). For example, the dominant copepods in Lake Macquarie in 1954 were *Acartia clausii (cf. Acartia (Acartiura)* sp.), *Paracalanus parvus* (now *P. indicus*) and *Temora turbinata*, with other major contributors including *Centropages* spp., *Tortanus barbatus*, and *Sulcanus conflictus* (Kott 1955). Furthermore, *Penilia avirostris* and species of *Podon* and *Evadne* were also present in Lake Macquarie.

Penilia avirostris was by far the most abundant taxa in the macrozooplankton of the lower Swan Estuary, which in part reflects the fact that it is larger (Smirnov and Timms 1983) than many of the copepods. Concentrations of similar magnitude to those of *P. avirostris* in the present study were recorded in the early 1970s in Cockburn Sound, a large marine embayment 25 km to the south of the Swan Estuary (Environmental Resources of Australia 1971, 1973). Examination of samples collected with 500 µm-mesh on the southern coast of Western Australia demonstrated that *P. avirostris* was often the dominant component of the macrozooplankton in the waters of this region (Fletcher and Gaughan, unpublished data). *Penilia avirostris* was also a numerically important component of the zooplankton in Lake Macquarie and Port Hacking in eastern Australia (Kott 1955; Griffiths 1983) and has been recorded in marine embayments in Australia as far north as Shark Bay on the west coast and Moreton Bay in Queensland on the east coast (Kimmerer *et al.* 1985; Davie 1990). This cladoceran is thus widely distributed in Australia and is seasonally abundant in the nearshore waters of southern Australia. It has also been recorded in inshore marine waters of north-eastern North America and Japan (Maurer *et al.* 1978; Madhupratap and Onbé 1986).

The larval stages of benthic or bentho-pelagic crustaceans were well represented in the macrozooplankton of the lower Swan Estuary. The zoeal stages of anomuran and brachyuran crabs and the mysis-stage larvae of other decapods were relatively abundant in the plankton. Likewise, large numbers of crab zoea have previously been recorded from estuaries in Victoria, New South Wales and North America (Rochford 1951; Kott 1955; Arnott and Hussainy 1972; Maurer *et al.* 1978). The relatively small number of mysids recorded in the lower Swan Estuary contrasts with the situation in the Peel-Harvey Estuary (Lukatelich, 1987) and in many southern African estuaries, where they are one of the most abundant taxa in the zooplankton (Grindley 1981).

The most abundant species in the macrozooplankton of the lower Swan Estuary represented marine taxa. The ichthyoplankton of the lower Swan Estuary also largely consists of marine species, with the larvae of only two of the eleven most abundant species belonging to teleosts which spawn within the estuary (*cf.* Loneragan *et al.* 1989; Gaughan *et al.* 1990; Neira *et al.* 1992). This situation contrasts with the zooplankton found in the basins of the Swan and Peel-Harvey Estuaries, where the estuarine copepods *Sulcanus conflictus* and *Gladioferens imparipes* are abundant (Bhuiyan 1966; Rippingale 1987; Lukatelich 1987). This contrast emphasises that, apart from during the winter and early spring, the lower reaches of the lower estuary remain at full strength sea water throughout each tidal cycle and can thus be regarded as essentially a marine embayment.

Distribution and seasonality

The data presented in this paper clearly demonstrate that, during the present study of the lower Swan Estuary, the abundance of macrozooplankton peaked in mid-summer, and decreased upstream from the estuary mouth. Furthermore, the abundance of each of the seven most abundant taxa within the macrozooplankton also decreased in an upstream direction, which implies that these taxa originated from surrounding marine waters or within Fremantle Harbour. This conclusion is consistent with the fact that all of the major macrozooplankton species were marine.

Although the tidal amplitude in the lower Swan Estuary is small (Spencer 1956), the amount of water movement would still be sufficient to transport some planktonic organisms backwards and forwards within this part of the system. The marked decrease in abundance of the macrozooplankton in an upstream direction in the Swan Estuary presumably reflects the progressive and rapid dilution of marine water as it mixes with estuarine water after being drawn into the river by tidal action, a situation paralleling that observed for the larvae of marine teleosts in the lower Swan Estuary (Gaughan *et al.* 1990). The upstream dispersal of marine zooplankton has been recorded in estuaries elsewhere in the world (*e.g.* Ketchum 1954; Barlow 1955) and, as in the lower Swan Estuary, the intrusion of marine plankton into at least some eastern Australian estuaries is limited (Kott 1955; Nyan Taw and Ritz 1978). Bayly (1975) has also noted that, although many inshore marine and marine euryhaline species have been recorded from estuaries in eastern Australia, they are usually not numerically important within these systems.

Besides tidal transport, it is also important to recognise that, during the spring and early summer, there is an overall net upstream movement of marine water through the lower estuary as the rate of freshwater discharge declines. This movement accounts for the marked rise in salinity that occurred at particularly the most upstream site (C) during the present study. This in turn almost certainly helps account for the increase that occurred in the abundance of the predominantly marine macrozooplankton at site C during that period.

Although the trend towards an increasing abundance of macrozooplankton during the spring and early summer at the two downstream sites is paralleled by that at the upstream site, but not of course to the same degree, the same parallel was not found in April, when marked increases in the macrozooplankton at sites A and B were not recorded at site C. It is thus relevant that, by April, the salinities throughout the lower estuary had stabilised at full strength sea water (Figure 1) and there is thus no longer a net upstream movement of marine water (see also Spencer 1956).

The progressive increase that occurred in the abundance of macrozooplankton at all three sites in the lower Swan Estuary between October and January paralleled the trends in both water temperatures and surface salinities, as these variables rose towards their annual maxima over this period. The ichthyoplankton, which is likewise dominated by marine taxa, also increased in abundance over this period (Gaughan *et al.* 1990).

The marked decline in the abundance of macrozooplankton in February may have been in part related to an unusually large discharge of water from the estuary on the day of sampling, and which occurred as a result of a marked increase in barometric pressure following several days when it had been relatively low. However, since the abundance of macrozooplankton recovered only slightly in the following month, and then only at sites B and C, the relatively low concentrations in February and March are more likely to reflect a late summer decline in the abundance of macrozooplankton in the marine waters outside the estuary. The marked rise in the abundance of macrozooplankton at sites A and B in April could thus represent the type of autumnal peak in zooplankton production that occurs in temperate marine waters of the Northern Hemisphere (Heinrich 1962). The seasonal trends recorded at sites A and B contrast with those exhibited by the zooplankton in the basins of the Peel-Harvey Estuary, where the peaks occurred in winter/early spring when the density of phytoplankton was high (Lukatelich, 1987).

The limited intrusion of marine macrozooplankton through the length of the lower Swan Estuary was paralleled by the restricted intrusion of estuarine species downstream into this part of the estuary. Thus, estuarine species, such as the calanoid copepods *Gladioferens imparipes* and *Sulcanus conflictus*, which are usually restricted to waters with salinities of less than 25‰ and have been found in large numbers in the middle Swan Estuary (Rippingale and Hodgkin 1974), were recorded in the lower estuary only during winter and spring when salinities were greatly reduced. The small numbers that were present in the lower estuary at that time had presumably been transported downstream by seasonally high discharges of fresh water.

Macrozooplankton as a food source for clupeoid fishes

Sardinops neopilchardus, Engraulis australis and *Hyperlophus vittatus* are at least intermittent planktivores and each feeds on copepods and *P. avirostris*, presumably by filtering these crustaceans from the water. Certain morphological characteristics of the cladoceran *Penilia avirostris, e.g.* the large antennae which protrude forward from the body, would presumably make this species highly susceptible to capture by filtering mechanisms. The large concentrations of *P. avirostris* may therefore represent a major food source for the above clupeoids in south-western Australian waters during summer.

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